

Semiochemically Mediated Foraging Behavior in Beneficial Parasitic Insects

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Chemical cues enable female parasitic wasps to locate the eggs, larvae, or other life stages of the insects in or on which they place their eggs. These chemical signals, or semiochemicals, may be produced by the hosts and/or by the plants on which the hosts feed. The composition of the chemical signal often differs with different species of hosts or with different plants. New evidence suggests that the wasps exploit semiochemicals emitted by plants in response to insect herbivore feeding. The wasps learn to respond to the different blends of chemicals that indicate the location of their hosts and they can be trained to respond to a specific odor blend. Thus, it may be possible to increase their effectiveness for biological control by conditioning them, prior to their release, to search for a target pest in a particular crop. © 1993 Wiley-Liss, Inc.

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INTRODUCTION

There have been several demonstrations of the practical value of entomophagous insects in controlling insect pests [1–3]. Many of these have involved the importation and establishment of a parasitoid in an area infested by a pest. Others entailed the release of large numbers of mass-produced parasitoids into an infested area or enhancement of abundance and/or efficiency of native or introduced beneficial species in an area. However, the vast potential of parasitoids for biological control has not yet been tapped. In today's agriculture we must enlist the aid of beneficial insects and other natural enemies to control insect pests. To do this effectively and economically we must first understand how these beneficial insects function. Then, we need to begin developing more effective ways to use them for biological control, based on our knowledge of their behavior and the factors that mediate that behavior.

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A key factor in achieving a high level of parasitization in a pest population is the ability of the female parasitoids to locate hosts. There are three major sources of intrinsic variation in the behavior of individual parasitoids that impact foraging. One source is genotypically fixed differences among individuals that are adapted for different foraging environments. Another source of variation is the parasitoids' physiological state relative to such needs as food and mating. The third source is the phenotypic plasticity of individuals, which permits behavioral modification through learning in response to different foraging situations. The parasitoids' effectiveness in locating and attacking hosts is determined by the net combination of these factors together with the conditions of their foraging environment [4].

SEMIOCHEMICALLY MEDIATED FORAGING

Semiochemicals, chemical signals that convey information between organisms [4], play a major role in enabling parasitoids to locate, identify, and exploit their hosts. A cursory examination of parasitoid-host relationships might suggest that the chemical signals that indicate the location and suitability of a host to a parasitoid would be highly specific and direct. Certainly, when a parasitoid specializes on one or a few closely related host species, and especially when those hosts are polyphagous, it would seem that searching for a host-specific kairomone would be the most efficient way for the parasitoids to find their hosts. However, potential hosts that escape detection are favored, and thus an evolutionary as well as a contemporary game of hide and seek imposes a variety of selection pressures on this system. Since the hosts tend to be inconspicuous, indirect cues to their location are often the only information available to the foraging parasitoid female. Additionally, over time, semiochemicals may vary, particularly with herbivorous hosts. As the hosts and the plants grow and change, the semiochemicals emanating from this host-plant complex change. Furthermore, the parasitoid may be required to search for hosts on different plants, or in a varied plant habitat, or generalist parasitoids may find different host species on the same plant. A variety of semiochemicals will be produced in these different situations. Finally, since nearly all these cues are indirect, both their nature and reliability will vary with the distance from the host. Thus, at a great distance the semiochemicals may only convey the information that a habitat is likely to contain suitable hosts. As the parasitoid gets close, different semiochemicals emanating from damaged plants or from feces or other host by-products give a much more direct and reliable indication of the availability and location of the host. In fact, the searching parasitoid utilizes a dynamic continuum of semiochemicals to locate and exploit her hosts [5,6].

EXPERIENCE AND LEARNING

In such a complex chemical environment a simple, rigid, kairomonally regulated search procedure would not permit parasitoids to exploit the available resources to the fullest extent. They must be able to detect a great variety of semiochemicals and to interpret the signals and determine their

significance in the context of the surrounding environment. In some instances they will even encounter different host species or growth stages of varying suitabilities in the same location. They often must choose between continuing to search in a given area or searching for a more productive area. The probability of their progeny surviving will depend on the choices made during foraging. Thus, these animals must have highly sophisticated and flexible foraging capabilities. They must be able to benefit from their experiences and learn in order to exploit these complex systems. It is therefore not surprising that these capabilities have recently been demonstrated in several species [7–10].

The complexity and variability of the semiochemicals that mediate parasitoid foraging dictate that a female must benefit from each experience during the relatively short time in which she can forage for hosts. We also might predict that experience should function in two ways in increasing the parasitoids' effectiveness during foraging. After an experience in which a host is located and parasitized, the parasitoid's motivation to search for other hosts should be greatly increased. This might be thought of as a priming effect, in that the parasitoid is primed to subsequently respond more strongly to cues, even though they may not be associated with the experience, which she recognizes as indicators of the presence of her host. Also, during the experience the parasitoid should learn several things associated with the host, including the semiochemicals it produces or those produced because of its presence in that particular environment. Subsequently, the parasitoid would be more likely to respond to those particular cues associated with her host during that experience than to semiochemicals that she had not yet experienced.

Somewhat surprising was the discovery that parasitoids need not come into direct contact with their hosts to obtain the experience necessary to increase their propensity to search and to learn chemical cues associated with their hosts. It has now been demonstrated with at least three species of parasitoids that brief contact only with host by-products results in increased response to odors of their hosts [7,11,12]. Thus, the wasps innately recognize specific semiochemicals in feces or other by-products that indicate the presence of hosts and they associate the odors of the substrate with the host-specific semiochemicals. Subsequently, they use these odors as cues in their search for hosts. This phenomenon provides a valuable way of finding hosts or prey species and may be widespread in parasitic and predatory systems where the target organisms, but not their by-products, often elude the searching parasitoid or predator.

The host recognition kairomone, which acts as the unconditioned stimulus in the associative learning process, also has a priming function in at least some species. *Microplitis croceipes* females given only a single experience on artificial diet fed *Helicoverpa zea* larvae and their feces (with or without an oviposition) responded strongly in a wind tunnel to extracts of feces from larvae fed cotton or other plants [13]. Since even inexperienced wasps respond to a limited degree to the extracts of feces from plant-fed hosts, but not to extracts of feces from hosts fed artificial diet, they probably have a strong innate preference for the odors of certain plants and only need priming to respond to these

preferred odors [9]. However, when the wasps were given several (two or more) experiences on larvae fed cowpea leaves they learned to respond preferentially to the odor of feces from cowpea-fed larvae when given a choice between the extracts of feces from larvae fed cowpeas or cotton [13]. Similarly, those given multiple experiences on larvae fed cotton preferred the odor of feces from cotton-fed larvae.

Priming on contact with host feces or other by-products probably serves as a safeguard to increase the probability that the parasitoid female will find her first host. Herard et al. [14] showed that contact with a substance on their cocoons immediately after adult emergence increased the subsequent response levels of *Microplitis demolitor* (Wilkinson) females. Thus a female emerging from her cocoon in the field gains experience that increases her motivation to search for certain preferred chemical cues when she is ready to oviposit. Then, when she finds feces or other substances that she recognizes by the presence of specific semiochemicals as by-products of her host, she is conditioned to search more intensely for the particular volatile chemical cues associated with those by-products. This system provides the wasp with the greatest probability of success in locating her hosts.

ACTIVE ROLE OF PLANTS

Although parasitoids can detect semiochemicals from undamaged plants and use these cues to locate the habitat or possibly even the micro-habitat of their hosts, there are distinct advantages to the parasitoid's ability to detect, differentiate, and respond to semiochemicals that distinguish plants damaged by their hosts from the surrounding environment. When the hosts feed on a plant, the plant produces and releases relatively large amounts of volatile chemicals. These chemicals provide very convenient cues that enable the parasitoids to detect and locate their hosts. These chemical cues will vary considerably depending on the species of herbivorous insect and the species, variety, age and growth stage of the plant on which it feeds. Therefore, they provide very specific information about the identity, location and possibly even the age or condition of the host.

Not only do parasitoids benefit from the semiochemicals emitted by damaged plants, but the plants also benefit when natural enemies that destroy their herbivorous attackers are attracted. Recently, Dicke, Sabelis and coworkers [15–18] have presented evidence that strongly indicates that plants infested with spider mites produce and emit volatile chemicals that attract other species of mites that prey on the infesting spider mites. They identified several compounds in volatiles from spider mite-infested lima bean leaves that were not present in the volatiles from uninfested or artificially damaged leaves. Four of these compounds, linalool, (*E*)- β -ocimene, (3*E*)-4,8-dimethyl-1,3,7-nonatriene, and methyl salicylate, attract the predatory mites and thus appear to act as synomones [18,19].

Similarly, we have recently shown that plants, when damaged, actively produce volatile chemicals in response to a substance produced by the attacking herbivores. We [20–23] have demonstrated that plants produce chemicals in response to damage by larvae of several lepidopteran species and

that females of the generalist larval parasitoid *Cotesia marginiventris* (Cresson) learn to take advantage of the plant-produced volatiles to locate hosts after experiencing these volatiles in association with hosts or host by-products. For example, the feeding of beet armyworm, *Spodoptera exigua* Hübner, larvae on corn seedlings results in the release of large amounts of volatiles. The composition of these volatiles varies with the length of time that the larvae feed. Immediately after the larvae begin feeding, the more volatile green leafy aldehydes and alcohols are released and continue to be released as long as the larvae are actively feeding. However, several hours after damage, the composition of the volatiles released from the plant changes and more compounds of higher molecular mass, primarily terpenoids, are released. Undamaged plants or artificially damaged plants release very little of these compounds, but artificially damaged plants that are treated with larval regurgitant release these compounds in about the same amounts as the larval damaged plants. Experienced *C. marginiventris* females respond to larvae-damaged plants and to artificially damaged plants treated with larval regurgitant more strongly than to undamaged or untreated artificially damaged plants [20,22]. They also respond to a synthetic blend of the compounds identified in the volatiles from damaged corn [23].

Recently, we found that in a wind tunnel, experienced *Microplitis croceipes* females are strongly attracted to volatiles produced by plants in response to feeding by their hosts, corn earworm larvae (McCall et al., unpublished). Thus, it appears that volatiles released by herbivore-damaged plants may play a key role in guiding *M. croceipes* females to their hosts, although, as indicated earlier, they also respond to volatiles from host feces. Although only a few examples of such synomonal plant-insect interactions have been discovered, it is likely, in the light of the adaptive advantages to both the parasitoids and the plants, that they are common in these types of tritrophic systems.

APPLICATION IN BIOLOGICAL CONTROL

Regardless of the approach used to employ parasitoids for biological control, knowledge of the mechanisms governing their host foraging behavior will be important to the success of the program. The successful establishment of imported species may be greatly facilitated if the release is designed so that the parasitoid females will have the greatest chance of locating a suitable host as quickly as possible. Conditioning the parasitoids to recognize and search for hosts by exposing them to semiochemicals associated with their hosts in the new location could greatly enhance their chances for success. This is particularly true if hosts in the new location are feeding on species or strains of plants different from those on which they fed where the parasitoids were collected.

When parasitoids are reared in the laboratory for subsequent release in the field to control insect pests, conditioning becomes very important. All research to date indicates that laboratory-reared parasitoids are ill-equipped to efficiently locate their hosts in the field. The rearing procedures used in nearly all parasitoid production facilities prevent the parasitoids from gaining the experience they need to forage effectively in the field. Therefore, it is very

important that these parasitoids be conditioned to search for semiochemicals produced when their target hosts feed on the plants to be protected.

Another problem critical to success in biological control is our inability to retain parasitoids in an area and stimulate continued foraging when pest populations are low. There is a certain host density threshold below which the probability of finding a host is so low that it is advantageous to search for an area with a higher host density. However, at low host population densities, the parasitoids could be most effective in managing pest populations if they could be induced to continue foraging. Recent research in our laboratories [24, and unpublished] indicates that it should be possible to manage parasitoid behavior to achieve maximum effectiveness at low host population densities by applying semiochemicals.

While a considerable amount of practical development must occur before the methods outlined above can be put into practice, it is clear that, in principle, parasitoids can be managed to enhance their effectiveness as biological control agents. With the rapid loss of available pesticides now occurring, it is imperative that we develop the necessary technology for effective biological control methods as quickly as possible. Manipulating the behavior of parasitoids to improve their foraging effectiveness will clearly be an important component of any future Integrated Pest Management (IPM) program employing these agents.

LITERATURE CITED

1. Clausen CP: Introduced parasites and predators of arthropod pests and weeds: A world review. USDA, Washington, DC, 545 pp (1978).
2. Sailer RI: Our immigrant insect fauna. **Bull Entomol Soc Am** 24, 3 (1978).
3. Hoy MA, Herzog DC: Biological control in agricultural IPM systems. Academic Press, New York, 589 pp (1985).
4. Law JH, Regnier FE: Pheromones. **Ann Rev Biochem** 40, 533 (1971).
5. Lewis WJ, Vet LEM, Tumlinson JH, van Lenteren JC, Papaj DR: Variation in parasitoid foraging behavior: Essential element of a sound biological control theory. **Environ Entomol** 19, 1183 (1990).
6. Vinson SB: The behavior of parasitoids. In: *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*. Kerkut GA, Gilbert LI, eds. Pergamon, New York, vol. 9, pp 417-469 (1985).
7. Lewis WJ, Tumlinson JH: Host detection by chemically mediated associative learning in a parasitic wasp. **Nature** 331, (1988).
8. Van Alphen JJM, Vet LEM: An evolutionary approach to host finding and selection. In: *Insect Parasitoids*. Waage JK, Greathead DJ, eds. Academic Press, London, pp 23-61 (1986).
9. Vet LEM, Lewis WJ, Papaj DR, van Lenteren JC: A variable-response model for parasitoid foraging behavior. **J Insect Behav** 3, 471 (1990).

10. Turlings TCJ, Wackers F, Vet LEM, Lewis WJ, Tumlinson JH: Learning of host-finding cues by hymenopterous parasitoids. In: *Insect Learning: Ecological and Evolutionary Perspectives*. Papaj DR, Lewis A, eds. Chapman and Hall, New York, pp 51–78 (1992).
11. Turlings TCJ, Tumlinson JH, Lewis WJ, Vet LEM: Beneficial arthropod behavior mediated by airborne semiochemicals. VIII. Learning of host related odors induced by a brief contract experience with host by-products in *Cotesia marginiventris* (Cresson), a generalist larval parasitoid. **J Insect Behav** 2, 217 (1989).
12. Vet LEM, Groenewold AW: Semiochemicals and learning in parasitoids. **J Chem Ecol** 16, 3119 (1990).
13. Eller FJ, Tumlinson JH, Lewis WJ: Effect of host diet and preflight experience on the flight response of *Microplitis croceipes* (Cresson). **Physiol Entomol**, 17, 235–240 (1992).
14. Herard F, Keller MA, Lewis WJ, Tumlinson JH: Beneficial arthropod behavior mediated by airborne semiochemicals. IV. Influence of host diet on host-oriented flight chamber responses of *Microplitis demolitor* (Wilkinson). **J Chem Ecol** 14, 1597 (1988).
15. Dicke M, Sabelis MW: How plants obtain predatory mites as bodyguards. **Neth J Zool** 38, 148 (1988).
16. Dicke M, Sabelis MW: Does it pay plants to advertise for bodyguards? Towards a cost-benefit analysis of induced synomone production. In: *Variation in Growth Rate and Productivity of Higher Plants*. Lambers H, Cambridge ML, Korings H, Pons TL, eds. SPB Academic Publishing bv, The Hague, Netherlands, pp 341–358 (1989).
17. Dicke M, van Beek TA, Posthumus MA, Ben Dom N, Van Bokhoven H, De Groot AE: Isolation and identification of volatile kairomone that effects acarine predator-prey interactions: Involvement of host plant in its production. **J Chem Ecol** 16, 381 (1990).
18. Dicke M, Sabelis MW, Takabayashi J, Bruin J, Posthumus MA: Plant strategies of manipulating predator-prey interactions through allelochemicals: Prospects for application in pest control. **J Chem Ecol** 16, 3091 (1990).
19. Nordlund DA, Lewis WJ: Terminology of chemical releasing stimuli in intraspecific and interspecific interactions. **J Chem Ecol** 2, 211 (1976).
20. Turlings TCJ, Tumlinson JH, Lewis WJ: Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. **Science** 250, 1251 (1990).
21. Turlings TCJ: Semiochemically mediated, host-searching behavior of the endoparasitic wasp *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae). Ph. D. Dissertation, University of Florida, Gainesville, 178 pp (1990).
22. Turlings TCJ, Tumlinson JH, Eller FJ, Lewis WJ: Larval-damaged plants: Source of volatile synomones that guide the parasitoid *Cotesia marginiventris* to the micro-habitat of its hosts. **Entomol Exp Appl** 58, 75 (1991).
23. Turlings TCJ, Tumlinson JH, Heath RR, Proveaux AT, Doolittle RE: Isolation and identification of allelochemicals that attract the larval parasitoid *Cotesia marginiventris* (Cresson) to the micro-habitat of one of its hosts. **J Chem Ecol** 17, 2235 (1991).
24. Lewis WJ, Martin WR, Jr: Semiochemicals for use with parasitoids: Status and future. **J Chem Ecol** 16, 3067 (1990).